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THE WINGS OF INSECTS.

J. H. COMSTOCK AND J. G. NEEDHAM.

CHAPTER III (*Continued*).

IX. THE VENATION OF THE WINGS OF HYMENOPTERA.

The Hymenoptera belong to the series of orders in which the direction of specialization of the wings results in a reduction in the number of the wing-veins. This is true of the wing as a whole, the reduction taking place in the anal area of the wing as well as in the pre-anal area. We have found no representative of the order in which all of the veins have been preserved ; and in the more specialized forms nearly all of the veins have disappeared.

A study of all of the families of the order shows that the most generalized of living forms, so far, at least, as concerns the structure of the wings, are to be found in the families Siricidæ and Tenthredinidæ. In these we find a close approximation in the number of wing-veins to the hypothetical type. But even here the courses of the branches of the forked veins have been greatly modified. These changes have been so great that the determination of the homologies of the wing-veins in this order was one of the most difficult problems of the kind that arose in the course of the study of the wings of insects.

This determination was made by the senior writer from an examination of the wings of adults before our present method of ontogenetic study was devised.[1] In the course of the present investigation we have endeavored to test the accuracy of his conclusions by a study of the tracheation of the wings of hymenopterous pupæ. We have found, however, that although the wings of the more generalized forms are abundantly supplied with tracheæ, the courses of these tracheæ have not been modified in the same way as have the courses of the veins with which they correspond. For this reason we are still forced to determine the homologies of the wing-veins by a comparative study of the wings of adults. We will, therefore, point out first what we believe to be the method of specialization of the wing-veins that has taken place in this order; and later we will discuss the nature of the changes that have taken place in the arrangement of the tracheæ.

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[1] Comstock, *Manual for the Study of Insects*, pp. 603–607.

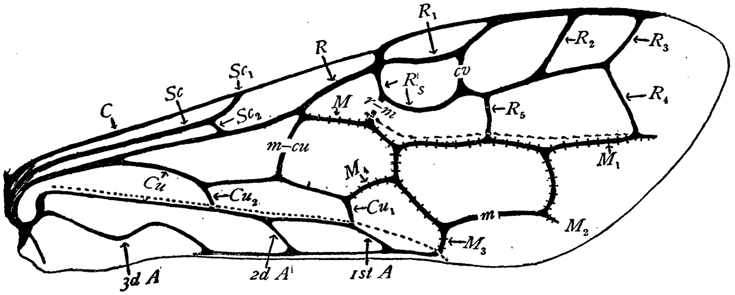

FIG. 38. — The veins of a typical hymenopterous wing.

The method of specialization of wing-veins which has taken place in the Hymenoptera can be most easily seen by a study of the fore wings of certain sawflies. The most useful for this purpose that we have found belong to the genera Pamphilius and Macroxyela. If we are right in our interpretation of the wings of these insects, there is preserved in each genus all of the primitive wing-veins with a single exception. And, as in each of these genera a different vein is lost, we are able to make a figure of a typical wing from a study of the two genera. Figs. 38 and 39 represent such a wing; in the former the veins are lettered; in the latter, the cells.[1]

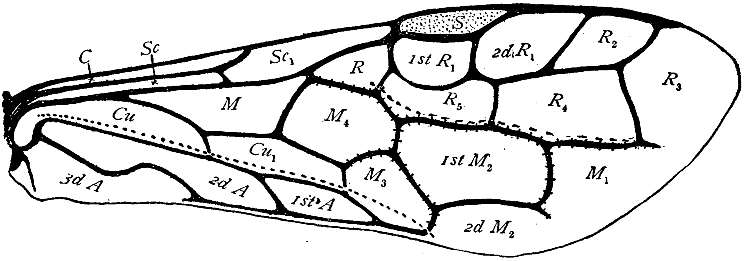

FIG. 39. — The cells of a typical hymenopterous wing.

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[1] Figs. 38 and 39 represent the venation of the fore wing of Pamphilius, except that vein R_2, which is lacking in this genus, is added. This vein is well preserved

In the wings of these sawflies the anal furrow and the median furrow are both well marked, and are in the typical positions; that is, the anal furrow is immediately in front of the first anal vein, and the median furrow in front of the media. The furrows are represented by dotted lines in the figures.

In the anal area the three typical veins are preserved; but they coalesce to a considerable extent, both at the base and near the margin of the wing.

In the basal part of the pre-anal area the stems of the principal veins are as follows: the costa coincides with the costal margin of the wing (Fig. 38, *C*); the subcosta (*Sc*) is well preserved and is forked; back of the subcosta is a strong stem formed by the coalescence of the other three veins; the cubitus (*Cu*) soon separates from this stem, extending in a curve towards the anal furrow; while the radius and the media coalesce for about half their length. In order to make these veins more distinct in the figure we have marked the free portion of the media with cross lines.

When we pass from the consideration of the main stems to a study of the branches, we meet a much more complicated problem, a problem which could not have been solved by a study of Hymenoptera alone. But a knowledge of the methods of specialization of the wings of Diptera gives a key to an understanding of the wings of Hymenoptera.

In the preceding article of this series we pointed out that in many Diptera there is a marked tendency for veins to coalesce from the margin of the wing towards the base. In the Hymenoptera this tendency is much more marked and has been carried to a much greater extent, resulting in a very complicated arrangement of wing-veins, even in the most generalized members of the order.

If the reader will examine the series of figures illustrating the coalescence of veins Cu_2 and *1st A* in the Diptera,[1] he will find it easy to understand what has taken place in the Hymenoptera. In the Hymenoptera, however, both branches of the

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in Macroxyela but in Macroxyela vein Cu_2 is lost. See Comstock, *Manual for the Study of Insects*, p. 606, for figures of the wings of these two genera.

[1] *American Naturalist*, vol. xxxii, No. 377, pp. 338, 339.

cubitus coalesce with the first anal vein; and this coalescence has proceeded so far that both branches cross the anal furrow and end in the anal vein remote from the margin of the wing.

It should be noted that vein Cu_2 is rarely preserved in this order, even in the more generalized forms. We have found it only in the genus Pamphilius. In Macroxyela[1] the position of the fork of the cubitus is indicated by a bend in this vein.

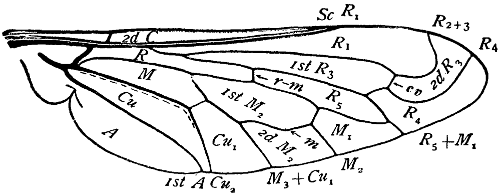

FIG. 40. — Wing of Pantarbes.

If the branches of the media be now examined, it will be seen that vein M_1 (Fig. 38) extends longitudinally near the center of the distal part of the wing, its primitive course being modified slightly if at all. Vein M_2 follows a course similar to the course of this vein in the dipterous genus Pantarbes (Fig. 40); so also does the medial cross-vein (Fig. 38, *m*). A comparison of the position of cells M_1, *1st* M_2, and *2d* M_2 in these two genera (Figs. 39 and 40) is very instructive.

Returning to Pamphilius (Fig. 38), we see that vein M_3 coalesces with the first anal vein, crossing the anal furrow near the margin of the wing. It is evident that the forces that are causing the branches of the cubitus to migrate along the first anal vein and towards the base of the wing are exerting a similar influence on this vein. It is also evident that vein M_4 and Cu_1

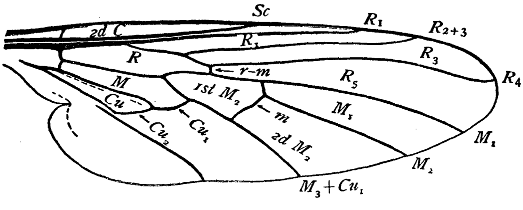

FIG. 41. — Wing of Rhamphomyia.

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[1] Comstock, *loc. cit.*, Fig. 735.

coalesce at the tip, and that the migration of the united tips of these veins (marked Cu_1 in the figure) towards the base of the wing has so modified the course of that part of vein M_4 which is still free that this part of this vein extends towards the base of the wing. This change is very similar to the change in the course of vein Cu_2 in the dipterous genus Rhamphomyia (Fig. 41).[1]

A curious result of this change in the direction of the course of vein M_4 is that the cell M_4 has been closed and pressed back to the center of the wing (Fig. 39, M_4), and now lies in front of the free portion of vein M_4 instead of behind it. A somewhat similar modification of cell M_3 has been pointed out in the Diptera; we repeat the figure of the wing of Eulonchus for comparison (Fig. 42).

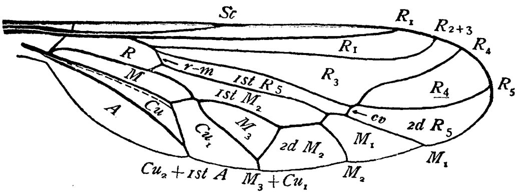

FIG. 42. — Wing of Eulonchus.

Let us now consider the courses of the branches of the radius. Here again we can gain help from a study of dipterous wings. Observe in Pantarbes (Fig. 40) the coalescence of the tips of veins R_5 and M_1. In the Hymenoptera a similar coalescence of veins R_5 and M_1 has occurred; but it has proceeded much farther, so that the free portion of vein R_5 in Pamphilius (Fig. 38, R_5) is remote from the end of the wing and has the appearance of a cross-vein.

In the Hymenoptera vein R_5 has been followed in its migration along vein M_1 by vein R_4, which has now reached a stage in Pamphilius that is quite similar to that reached by vein R_5 in Pantarbes. But like vein R_5 it has the appearance of a cross-vein. In the fore wing of the honey-bee (Fig. 43) veins R_4 and R_5 still retain the appearance of branches of a forked longitudinal vein.

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[1] At the time that the figures in Comstock's *Manual* were prepared it was believed that the media was typically three-branched. For that reason the vein which we now regard as vein M_4 was believed to be a cross-vein. The interpretation given above accords better with what we have since learned to be the typical form of the media.

In Pamphilius vein R_1 is curved away from the costal margin of the wing to make room for a stigma (Fig. 39, *S*), and vein R_3 ends in the costal margin a short distance before the apex of the wing (Fig. 38). Vein R_2 has been lost in this genus, but is well preserved in certain closely allied forms,[1] and is, therefore, represented in the figure.

While the tips of the branches of the radial sector have migrated away from the apex of the wing, the bases of these branches coalesce in the opposite direction; from these two causes results the transverse bracing of the radial area of the wing, which is a very characteristic feature of the venation of the wings in this order.

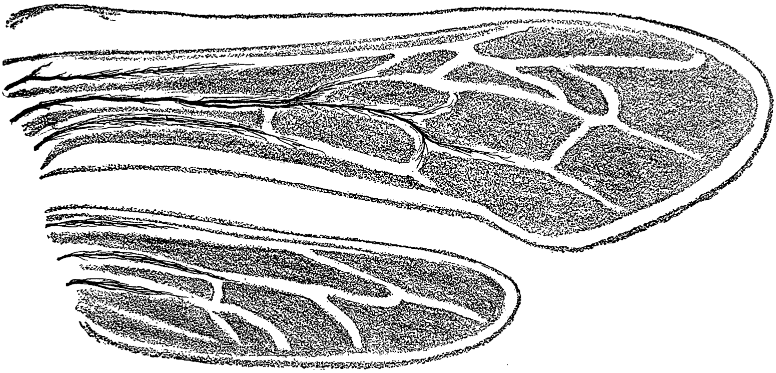

FIG. 43. — Wings of Apis.

The details of these changes will be made clear by an examination of Figs. 44 and 45. The former represents the primitive mode of branching of the radius; the latter, the radial area of the typical hymenopterous wing (Fig. 38). In the hymenopterous type veins R_{2+3} and R_{4+5} of the primitive type coalesce so far that the branches of the sector arise from a common stem; and the tips of all of them have moved away from the apex of the wing, veins R_2 and R_3 following the costal margin of the wing; and veins R_4 and R_5 following vein M_1. In the Hymenoptera a cross-vein has been developed between veins R_1 and R_s. But this is not a peculiarity of this order; a similar cross-vein exists in many insects, and has been represented in our figures of the wings of a nymph of Nemoura.[1]

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[1] See p. 414, footnote.

From the foregoing account it will be seen that even in the most generalized of living Hymenoptera there exists a highly modified wing venation. The indication of the details of the further modifications exhibited by the more specialized members of this order has already been done by one of us in another place. We will, therefore, merely refer to a single illustration.

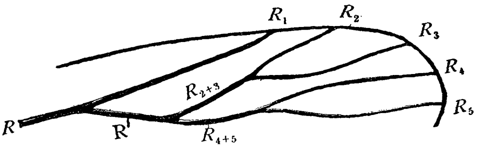

FIG. 44. — The typical radius.

When the fore wing of a honey-bee (Fig. 43) is examined it is found that, although this insect exhibits a wonderfully high development of instinctive powers, it retains a comparatively generalized wing venation. This wing, however, is much more modified than the fore wing of Pamphilius; and hence a comparison of the two is instructive.

In the honey-bee the subcosta is lost; so, too, is the second branch of the radius. Veins R_4 and R_5 retain a more generalized condition than do these veins in the sawflies. The coalescence of the radius and the media extends farther than in Pamphilius, the base of the free portion of the media being carried farther from the base of the wing than the medio-cubital cross-vein (*m-cu*). This results in the base of the free

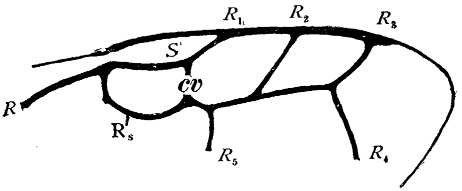

FIG. 45. — The radius in Hymenoptera

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[1] *American Naturalist*, vol. xxxii, January, 1898, pp. 46, 47.

portion of the media (M) being V-shaped. No trace of the second branch of the cubitus remains; and vein Cu_1 appears as a short cross-vein, extending to the anal furrow near the middle of its course. But the most striking modification of all is exhibited by vein M_4; the tip of this vein in its migration towards the base of the wing has passed over an arc of nearly 180°, so that now it extends from the point where it separates from vein M_3 directly towards the base of the wing, and joins the medio-cubital cross-vein.

X. THE TRACHEATION OF THE WINGS OF HYMENOPTERA.

In our studies of the wings of the more generalized insects we found a close correlation between the venation and the tracheation of the wings. It can be accepted as a firmly established fact that the courses of the wing-veins of primitive insects were determined by the courses of preëxisting tracheæ. And one of the principal objects of the present investigation was to endeavor to settle certain questions regarding the homologies of wing-veins by a study of the tracheæ that precede these veins.

The importance of this method of study has been well shown by the results which we have obtained. But we also found that in the Trichoptera[1] there is little correlation between the venation and the tracheation of the wings, a remarkable reduction of the wing-tracheæ having taken place. A similar reduction of the tracheæ of the wings exists in most families of Diptera; and even when a large proportion of the tracheæ are retained, as in certain Asilids, they afford little aid in the determining of the homologies of the wing-veins. For this reason we omitted a discussion of the tracheation of the wings of Diptera. Again, in the Hymenoptera we find that the courses of the tracheæ cannot be depended upon for determining the homologies of the wing-veins. But here, in the more generalized members of the order, we find a very complete system of wing-tracheæ; and it is, therefore, incumbent on us either to point out the correspondence between the tracheæ and the wing-veins, or to demonstrate that such a correspondence does not exist.

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[1] *American Naturalist*, vol. xxxii, April, 1898, p. 256.

In the introductory article of this series,[1] in discussing the figures of the wings of a nymph of Nemoura, we called attention to the fact that the tracheæ in the wings of that insect extend in straight lines or in gentle curves, while in some cases the corresponding veins are much more angular; and we offered the following explanation of this phenomenon:

> It is evident from this that in the perfecting of a wing as an organ of flight the position of a vein in the adult may become quite different from that of the corresponding trachea of the immature form. In other words, although there is no doubt that the courses of the principal wing-veins of primitive insects were determined by the position of the principal tracheæ of the wings, the wing-veins have been more or less modified to meet the needs of adult life; while at the same time the tracheæ of the immature wing, serving the purpose of respiration, and lying more or less free within the wing-sac, have not been forced to follow closely the changes in the cuticular thickenings of that sac.

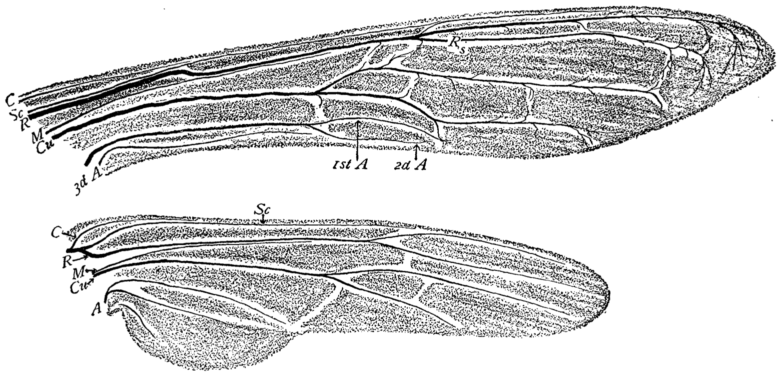

Fig. 46 — Wings of a pupa of Tremex.

In the Hymenoptera, as we have shown, the courses of the branches of the forked veins, in those forms where they have been preserved, have been so modified that these branches extend more or less transversely, making sharp angles with the main stems. It is not strange, therefore, that the tracheæ of the wings of the pupa lying free within the wing-sac, have not followed these changes.

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[1] *American Naturalist*, vol. xxxii, January, 1898, p. 47.

Fig. 46 represents the wings of a pupa of Tremex; and Fig. 47, the fore wing of a pupa of Apis. In both cases the main tracheæ extend in nearly direct lines from the base of the wing to near its outer margin. This fact alone would indicate that the needs of respiration of the pupa, rather than the flight function of the adult wing, has been the important factor in determining the courses of these tracheæ.

A comparison of the fore wing of Tremex with that of Apis shows a remarkable difference in tracheation. In Tremex vein R_s is traversed by a branch of the radial trachea (*R*); while in Apis the radial trachea is not branched, and the trachea traversing vein R_s arises from the cubital trachea (*Cu*). When this fact was first observed it was thought that the trachea of the radial sector in Apis had become transferred from the radial trachea to the cubital. We were not greatly surprised at this phenomenon, for a similar switching of tracheæ is common in those Lepidoptera in which the branches of the media become joined to the adjacent veins.

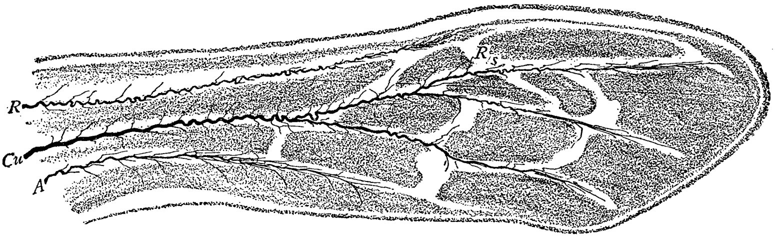

FIG. 47. — Fore wing of a pupa of Apis.

It was found, however, that this is not the explanation of the change. An examination of the wings of young pupæ of the honey-bee revealed the fact that in this insect the laying out of the wing venation precedes the tracheation of the wing. After the wing-veins reach that stage of development in which they appear as pale bands, the tracheæ grow out from the base of the wing into them. Fig. 48 represents the wings of a pupa taken at a stage which illustrates this pushing out of the tracheæ into the previously formed wing-veins.

It is obvious that tracheæ developed in this way will follow the paths offering the least resistance to their progress; and that it is not to be expected that the tracheæ will preserve their primitive arrangement under these conditions. This brings us to the conclusion, already announced, that in determining the homologies of the wing-veins in the Hymenoptera we are forced to base our conclusions on a study of the veins themselves, and that a method of study which is of the highest importance in determining the homologies of the wing-veins in many other insects, is of little use here for this special purpose.

We have pointed out a striking difference in the tracheation of the fore wings of Tremex and of Apis. An equally striking difference may exist between the fore and hind wings of the same insect. Thus in the pupa of Tremex (Fig. 46) the main stem of the radial trachea traverses the subcosta in the fore wing; while in the hind wing it retains its primitive position. In more specialized members of the order, as in the Ichneumon-flies, even less of the primitive arrangement of the tracheæ is preserved. But a further discussion of this phase of the question would not be profitable here.

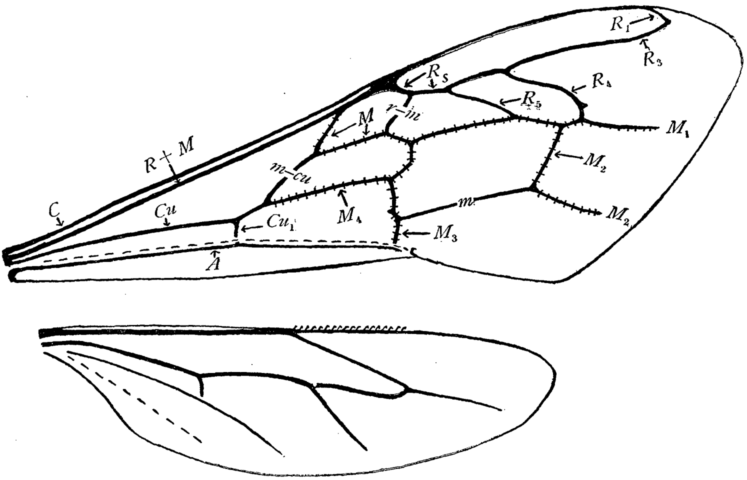

FIG. 48. — Wings of a young pupa of Apis.

XI. THE VENATION OF THE WINGS OF EMBIIDÆ.

The systematic position of the family Embiidæ is a question regarding which there is much difference of opinion. We do not purpose to discuss this question here beyond pointing out that in the structure of the wings there is little in common between these insects and the Blattidæ and Mantidæ, with which they have been associated by Brauer,[1] or with the Termitidæ or Psocidæ, with which they are grouped by Sharp.[2] If we were forced to decide regarding the rank of this family from a study of the wings alone, we would be obliged to regard it as representing a separate line of development of ordinal value. But in this place we wish merely to offer a suggestion regarding the probable homologies of the wing-veins.

Fig. 49 represents the fore wing of Oligotoma and is based on a figure by Wood-Mason.[3] If this figure is correct, there is little difficulty in recognizing the principal veins. The only difficulty is presented by the four transverse veins on the distal half of the wing. After what we have seen in the wings of Diptera and of Hymenoptera, the most obvious interpretation of these is that they are branches of the radius, the tips of which coalesce with vein M_1. The result of this coalescence is that these veins have come to appear like cross-veins, as do veins R_4 and R_5 in the Hymenoptera. There is this striking difference, however: in the Hymenoptera only two branches of the radius bend back and unite with vein M_1; in the Embiidæ all of the branches of the radius are modified in this way. And in the Embiidæ there is no indication of a similar backward bending of the branches of the cubitus.

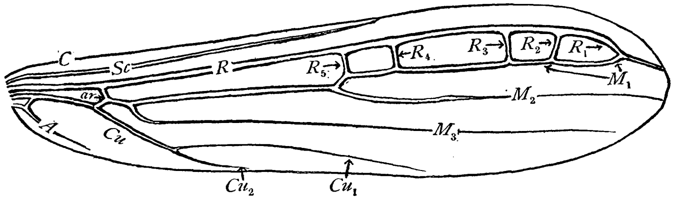

Fig. 49. — Wing of Oligotoma.

Entomological Laboratory,
Cornell University, January, 1898.

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[1] Friedrich Brauer, *Systematische-zoologische Studien*, p. 126.

[2] *The Cambridge Natural History*, vol. v, p. 342.

[3] *Proc. Zoöl. Soc. London*, 1883, p. 628.